

SPHAEROIDAL ENROLMENT AND THORACIC CHARACTERS IN *BELLELLA DEPRESSA* AND OTHER OLENID TRILOBITES

by H. B. WHITTINGTON

ABSTRACT. In sphaeroidal enrolment, the exoskeleton formed a closed capsule. Well known in post-Cambrian trilobites, many Cambrian species, in addition to Agnostina and eodiscoids, also enrolled in this manner. Characteristic features of such forms (other than Agnostina and eodiscoids) are: a fulcrate thorax; the fulcrum relatively close to the axis; the facets of the anterior segments large and backwardly directed; more posterior facets smaller, steeper, and less so directed. These features are described in detail in *Bellella depressa* and *Peltura scarabaeoides scarabaeoides*, and were shared by other olenids, including *Triarthrus*, in which sphaeroidally enrolled specimens are known. Other olenids, in which the fulcrum was distant from the axis, may have enrolled in the cylindrical manner, which left a lateral gap in the enrolled exoskeleton. The significance in classification of these and other characters of the thorax has yet to be evaluated in Olenidae and other groups.

SPHAEROIDAL enrolment, in which the exoskeleton forms a closed subspherical or ovoid form, is familiar in calymenids and *Phacops*. The tips of the thoracic pleurae and edge of the pygidium were tucked inside the cephalic doublure (calymenids), or in phacopids were accommodated in vincular notches and a groove in the cephalic doublure (e.g. Whittington 1992, pls 89, 115; Chatterton and Campbell 1993, figs 1a–f, 2a–c, e–g). In these and many other trilobites which enrolled in the same fashion, the thorax was fulcrate, the fulcrum situated in the adaxial half of the pleural width (tr.). The horizontal, inner portion of the pleura gave a precise, straight hinge, the anterior articulating flange fitting beneath the posterior flange of the preceding segment. The outer portion of the pleura was bent down and faceted, so that these portions overlapped one beneath the other in enrolment. The coaptative devices associated with the close fit between the tips of the pleurae and margin of the pygidium with the cephalon have been described in many species (e.g. Clarkson and Henry 1973; Henry and Clarkson 1975; Clarkson *et al.* 1977; Lespérance 1991; Chatterton and Campbell 1993). It is emphasized here that not only were such devices coaptative, but that the entire form of the exoskeleton was necessarily so – the convexity of its different portions, the width (tr.) and inclination of the outer portions of the pleurae, the size and inclination of the facets, and the shape of the cephalon *vis-à-vis* that of the thoracic segments and pygidium. Thus, for example, the anterior arch in the border of the cephalon, mentioned by Clarkson (1966, p. 82) as allowing the entry of respiratory and feeding currents when the animal was extended on the sea floor, must also have been shaped to accommodate the thoracic segments and pygidium in enrolment.

Sphaeroidal enrolment is known not only in the post-Cambrian trilobites referred to above, but also in the Lower Cambrian *Crassifimbra* (Palmer 1958), in Middle Cambrian ellipsocephalids (Westergaard 1936, pl. 11, fig. 9a–c; Geyer 1990) and in the Upper Cambrian examples described by Stitt (1983). The thorax was fulcrate, the outer portions of the pleurae faceted, and Palmer (1958, text-fig. 5) illustrated stops in the pleural doublures which limited overlap. Stitt emphasized the stronger backward deflection of the outer portions of the pleurae of the more anterior segments, the differing size and inclination of the facets, and that the flexure between the cephalon and anterior thoracic segments was strong. In Agnostina and eodiscoids (see Bergström 1973, p. 30) the

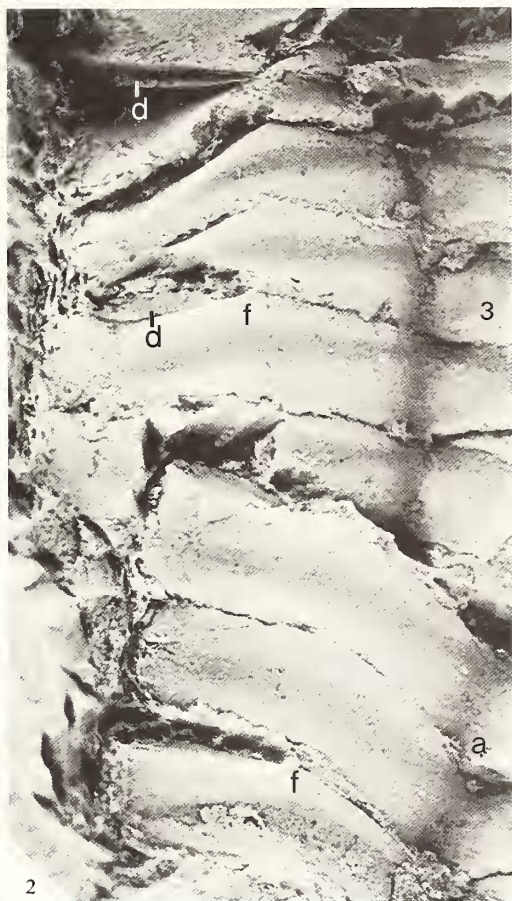
short thorax enabled the flat doublure of cephalon and pygidium to be brought into contact (Agnostina), or that of the pygidium to fit close inside the cephalic doublure (eodiscoids). Robison (1964, p. 515) described a vincular groove in the pygidial doublure of Agnostina, into which the inner edge of the cephalic doublure fitted on enrolment; Rushton (1966, p. 15) described vincular structures in eodiscoids. In both groups the thorax was fulcrate, but the outer portions of the pleurae did not overlap in enrolment, but fitted edge-to-edge against each other and the edges (or facet) of the cephalon and pygidium. To enable this fit the outer portions of the pleurae were narrow (tr.) and cut off by straight or curved edges anterolaterally and posterolaterally (Rushton 1966, text-figs 6, 8; Hunt 1967; Jell 1975; Whittington 1992, pls 55, 73). Robison (1964, p. 515) commented on the special shape of the segments in Agnostina and the lack of a doublure; the extremely narrow doublure in *Pagetia*, and the form of the segments were described by Jell (1975, p. 62).

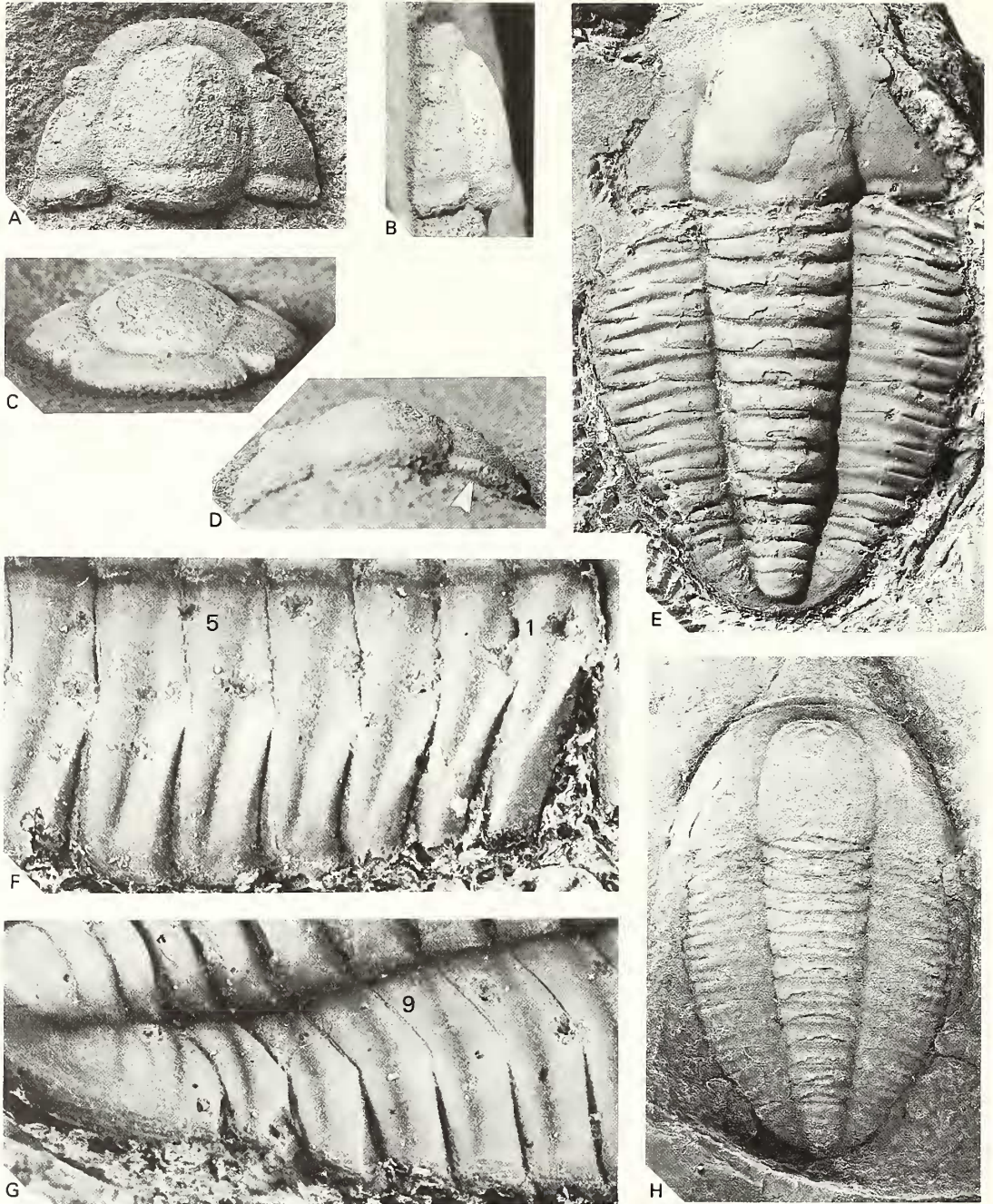
Sphaeroidal enrolment, then, is characteristic of many Cambrian trilobites. However, Fortey and Owens (1991*b*, p. 77) expressed the view that complete enrolment of the exoskeleton of *Beltella depressa* was not possible because flexure between posterior thoracic segments was limited and because these segments and the pygidium were not shaped to fit closely beneath the cephalon. Yet the fulcrate thoracic exoskeleton exhibits features noted above in trilobites that enrolled sphaeroidally, in particular the strong backward deflection of the large facets of anterior segments. Whether or not *B. depressa* could enroll sphaeroidally depended on the form of the entire exoskeleton. Here I contend (Text-fig. 2), on the evidence of the least flattened specimens, that the free cheeks were more steeply inclined than in Fortey and Owens' restoration (1991*b*, fig. 2), and that the outline of the thorax was slightly less convex abaxially. The convexity of the exoskeleton in Text-figure 2 is similar to that given to the closely related species *Leptoplastides salteri* by Fortey and Owens (1991*a*, fig. 9), and to that of *Peltura scarabaeoides scarabaeoides*. The illustrations of the latter species (Pl. 2) show the differences in appearance between an exoskeleton that has been relatively slightly flattened, and those of *B. depressa* (Pl. 1; Text-fig. 1E, H) which were originally of a similar convexity but have suffered much greater compaction. The differing size, shape and orientation of the facets on successive segments of these species appears to be coaptative, and to have enabled the greater flexure between anterior sclerites (and lesser between posterior sclerites) that facilitated the close-fitting enrolment.

Bergström (1973, p. 21) discussed enrolment in Olenidae, and concluded that many, possibly all, species were able to enroll. Clarkson's (1973, text-figs 2d-f, 5a-c, 6a-c, 7a-c, 8a-c) restorations revealed the strong convexity of the cephalon in certain species, and that of the entire exoskeleton was shown in Fortey's (1974) plates, and by those of the silicified material of Ludvigsen (1982). The latter author (p. 61) commented on the strong convexity of a species of *Parabolinella*, and the different appearance such material would have if it were flattened in shale. Among other details the doublure beneath the tips of the thoracic pleurae in *Parabolinella* (Ludvigsen 1982, pl. 49, figs *o, q*) are shown, and have a raised inner edge which may have provided a stop to enrolment at the posterior edge. In species of *Balnibarbi* (Fortey 1974, pl. 2, fig. 3; text-fig. 4), *Parabolinella*

EXPLANATION OF PLATE I

Figs 1-4. *Beltella depressa* (Salter in Murchison, 1859). 1-3, Lower Tremadoc, Clarenville Formation, south of mouth of Trilobite brook along south-west shore of Random Island, half-way between brook and Pelly's Mill, Newfoundland. 1-2, NHM It 20246; 1, internal mould of cranidium and partially disarticulated, incomplete thorax: dorsal view, articulating half ring of first segment has been exposed; $\times 3$; 2, oblique view of left side, showing mould of doublure (d) of posterior border of cranidium and left pleurae of segments 1-8, axial (a) and fulcral (f) articulating processes, and further preparation of tip of pleura of segment three (numbered) to show part of doublure (d) lying on facet of pleura of segment 4; $\times 8$. 3, NHM It 20229; posterior portion of external mould showing sculpture of last two thoracic segments and pygidium; $\times 5$. 4, BRSMG Cd 550a; Breadstone Shales, Gloucestershire; original of Fortey and Owens 1991*b*, pl. 1, fig. A; flattened exoskeleton lacking pygidium; $\times 3$.





TEXT-FIG. 1A-H, *Beltella depressa* (Salter in Murchison, 1859); Lower Tremadoc; Gloucestershire, England. A-D, BRSMG Cb 4400, original of Curtis 1968, pl. 9, fig. A; Micklewood Beds; cranium, internal mould, dorsal, left lateral, anterior and posterior (arrow points to fulcrum) views, respectively; $\times 3$. E-G, BRSMG Cc 860a, original of Fortey and Owens 1991b, pl. 1, fig. B; Breadstone Shales; E, dorsal view; $\times 3$; F-G, oblique right lateral views of thoracic pleurae 1-7 (segments 1, 5 numbered), and pleurae 8-12 (segment 9 numbered) and pygidium, respectively; $\times 8$. H, BRSMG Cc 2010, original of Fortey and Owens 1991b, pl. 1, fig. D; Breadstone Shales; dorsal view; $\times 2.6$.

(Ludvigsen 1982, fig. 49a–s), *Anaximander* (Fortey 1974, pl. 21, fig. 3), *Bienvillia* (Fortey 1974, pl. 22, fig. 1) and *Triarthrus* (Ludvigsen and Tuffnell 1983, pls 2–3) the thorax was fulcrate, the fulcrum one-third or less of the width (tr.) of the pleura from the axial furrow. The facet on the anterior four thoracic segments was large and backwardly directed, facets on succeeding segments were less backwardly directed. I consider that in species of the genera mentioned above sphaeroidal enrolment was probable. The only examples known to me of such an enrolled holaspid form are those of *Triarthrus beckii* figured by Ross (1979, pl. 1, figs 1–12; for justification of this specific name see Ludvigsen and Tuffnell 1983, p. 571); Ludvigsen (1982, fig. 50c) showed an enrolled meraspid of *Parabolinella panosa*, and Ludvigsen and Tuffnell (1994, pl. 3g) figure a partially enrolled *Triarthrus*. Fortey (1974, p. 27, fig. 4) considered that *Balnibarbi pulvurea* could enroll, presumably completely.

As Bergström (1973, p. 21) recognized, some olenids had a thorax of a different form. *Westergaardites* (Henningsmoen 1957, fig. 18) had 19 thoracic segments, each with a wide (tr.), horizontal inner portion and a narrow, spinose outer portion. In *Leptoplastus norvegicus* (Henningsmoen 1957, pl. 15, fig. 7), the inner, horizontal portion of each pleura was wide (tr.), the outer narrow and faceted, as it was in *Ctenopyge modesta* (Henningsmoen 1957, pl. 19, figs 5, 9–10); in *C. pecten* (Westergaard 1947, pl. 3, fig. 12) there were long pleural spines on the thorax. Such species may not have formed a closed capsule on complete enrolment, rather there would have been a lateral opening partially covered by spines. Bergström (1973, p. 14, fig. 8b) referred to this type of enrolment as cylindrical, illustrating it by a drawing of *Fallotaspis* (Olenellina), and a model of *Ctenopyge* (1973, pl. 1, fig. 8). Figured examples of this type of enrolment are rare, but one is of *Remopleurides perspicax* (Nikolaisen 1983, pl. 5, figs 1–5).

How important thoracic characters may be in classification of Olenidae, including the controversial subfamilial divisions (Fortey and Owens 1991b, p. 74), is an open question. The above discussion suggests that the position of the fulcrum, close to, or far from, the axial region, may be a useful character. Fortey (1974, p. 13) recognized the pleural node, a triangular inflated area of the posterior pleural band adjacent to the axial furrow, as characteristic of Balnibarbiinae. Ludvigsen and Tuffnell (1994, p. 192, fig. 12) regarded a similar inflation as a cardinal character in Triarthrinae. They interpreted this inflation as bounded posteriorly by a posterior pleural furrow, but this furrow is the change in slope between the inflation and the short (exs.) posterior articulating flange; this change in slope dies out distal to the fulcrum and is not analogous with the true pleural furrow. The pleural node is not developed in *Beltella* or *Peltura*: in the former the posterior pleural band is but gently inflated; in *Peltura* (Pl. 2, fig. 3) more strongly, and separated by a distinct change in slope from the posterior flange.

SYSTEMATIC PALAEOONTOLOGY

Family OLENIDAE Burmeister, 1844

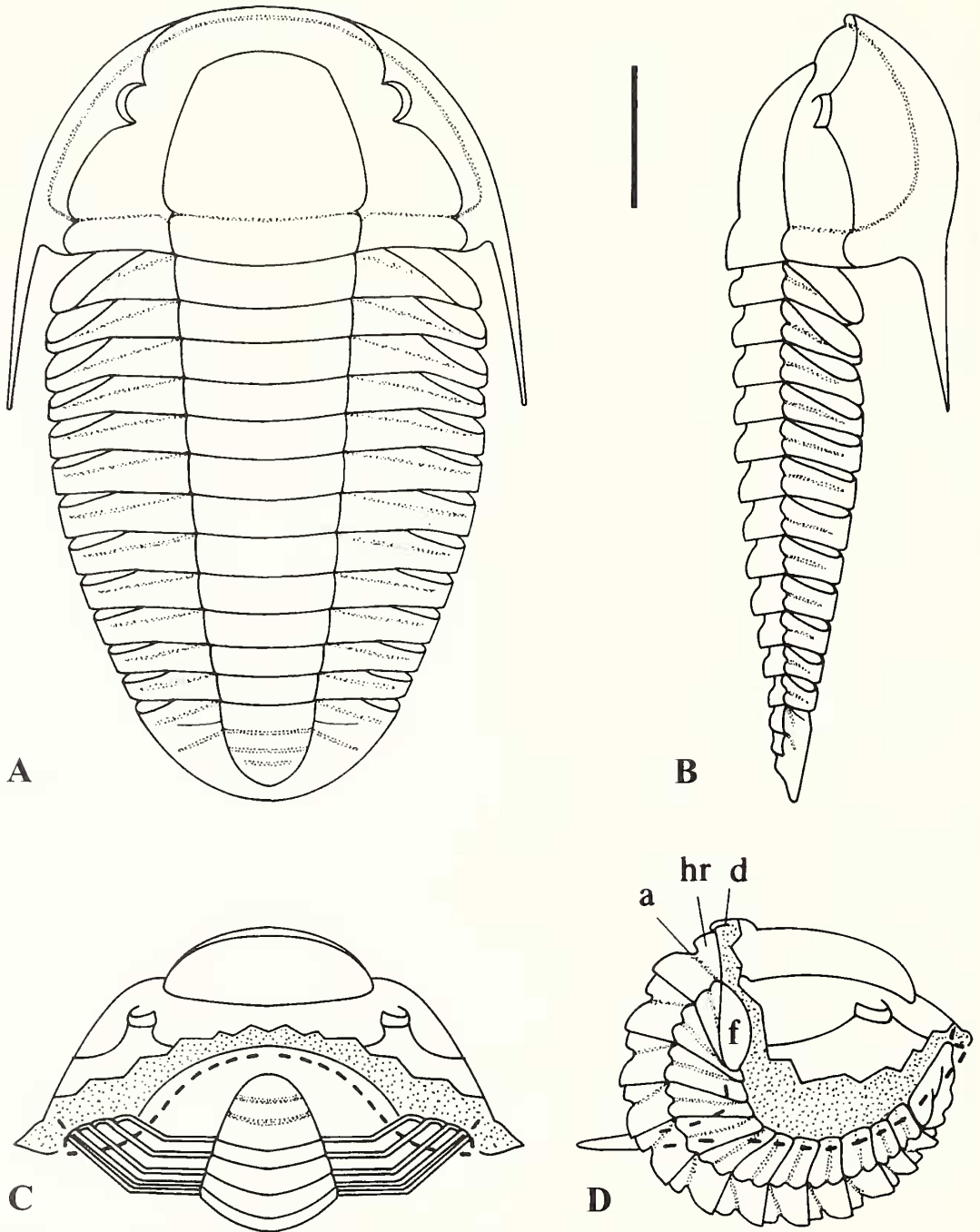
Genus BELTELLA Lake, 1919

Beltella depressa (Salter in Murchison, 1859)

Plate 1; Text-figures 1–2

Material. I accept the synonymy of this species as given by Fortey and Owens (1991b), and hence include material from the Breadstone Shales and Micklewood Beds of the Tortworth inlier, Gloucestershire, and from the Clarendon Formation, Random Island, Newfoundland, strata which are of Lower Tremadoc age.

Morphology. Fortey and Owens (1991b) described this species and referred to the effects of flattening on the original appearance of the exoskeleton; additional details are given herein and used in a new reconstruction (Text-fig. 2). The least flattened cranidium known (Text-fig. 1A–D) shows the minimum convexity of the cephalon, and that the posterior border had a horizontal inner portion, and was bent down at the fulcrum into a wider (tr.), downsloping outer portion. The free cheek conformed to this downslope and hence appears narrow (tr.) in dorsal view in one of the less flattened specimens from the Breadstone Shales (Text-fig. 1H); the trace of the genal spine continues the curve of the lateral border. In the original of Plate 1, figure 4, the free



TEXT-FIG. 2. *Beltella depressa*. A–B, restoration of extended exoskeleton in dorsal and right lateral views. C–D, restoration of enrolled exoskeleton in anterior and right lateral views. Heavy dashed line indicates margin of cephalon and doublure of cephalic border in section; parts of dorsal exoskeleton cut away to reveal tips of thoracic pleurae and edge of pygidium, and lateral view of first thoracic segment; interior of exoskeleton stippled. Abbreviations: a, articulating furrow; d, doublure of occipital ring; f, facet; hr, half ring. Scale bar represents 10 mm.

cheeks are spread out and pushed inwards, and the genal spine projects slightly outward, as it does in the originals of Stubblefield (*in* Smith 1933, p. 367, pl. 34, figs 10–11). This divergence from the lateral border may be the result of flattening. The mould of the doublure of the anterior border is preserved in the original of Text-figure 1H, as a narrow channel, and a similar narrow channel beneath the outer portion of the posterior border (Pl. 1, fig. 2) is the mould of the doublure. It is presumed that a narrow doublure, convex ventrally, also underlay the lateral border.

The thorax of 12 segments (Text-fig. 1E, H) was fulcrate, the inner portion of each pleura horizontal, the outer portion bent down at the fulcrum to slope in conformity with the posterior cephalic border. The long (sag.) articulating half ring of the first segment has been exposed in the partially disarticulated, flattened, incomplete Clarendon specimen (Pl. 1, fig. 1). In the succeeding four segments the axial rings are broken to expose a mould of the doublure of the ring, or of the half ring of the succeeding segment, or of a combination of both, as is the case in broken rings of other moulds (Text-fig. 1E, H). Each half ring was of similar length (sag.) to the axial ring in front of it, so that it reached the posterior slope of the articulating furrow. This furrow had a slight curvature, concave forward in dorsal view, a gentle posterior slope in profile, rising anteriorly vertically to the half ring. The anterior edge of the inner portion of each pleura bore an articulating flange (Pl. 1, fig. 2), which fitted beneath the posterior cephalic border or the posterior flange of the segment in front. The posterior flange is not visible in the internal mould (Pl. 1, fig. 2) because this edge is broken; on the external surface (Text-fig. 1F–G) the short (exs.) flange is defined faintly behind the gently convex posterior pleural band. An axial articulating process was situated where the axial furrow deepens at the posterior, adaxial end of the inner pleural portion (Pl. 1, fig. 2) and a fulcral process at the anterior abaxial end, with corresponding sockets at the extremities of the adjacent edges. The outer portion of each pleura had the posterior edge backwardly and outwardly directed, backwardly most strongly on the first segment, progressively less so on succeeding segments (Pl. 1, fig. 2; Text-fig. 1E–G). The anterior edge of the outer portion of the pleura was the steeply inclined facet, which appears to have had a concave surface. The size and shape of the facet changed along the thorax, those of the first three segments being largest, the posterior edge curved back so that the pleural furrow terminated against it. In more posterior segments the posterior edge of the facet was less strongly backwardly directed, and the pleural furrow extended behind the facet to die out close to the pleural tip. This change in form and direction of the facet meant that the shape of the outer portion of the pleura changed progressively backward (Text-fig. 1E–G), from short (exs.) and blade-like on the first segment to longer (exs.) and subparallel-sided posteriorly. The abaxial margin of the pleural tip of segments 4–12 was straight, the edge not sharp, but blunt as the dorsal exoskeleton curved under to meet the doublure. This blunt edge was terminated anteriorly by the facet, and, because the facet was concave, the anterior tip of the pleura curves forward at the posterolateral margin of the facet. Compaction caused the outer portions of some of the pleurae to be curved slightly, concave upwards, and flattened the tip. In such cases (e.g. segments 4–5, of Pl. 1, fig. 2; left side of Text-fig. 1E) this forward curvature at the anterior tip was exaggerated. I consider that this forward prolongation (Fortey and Owens, 1991*b*, p. 73) was too slight to have inhibited the pleurae in sliding one below the other in enrolment. The form of the pleural doublure could not be revealed completely in the moulds, but the fragment preserved (Pl. 1, fig. 2) suggests that it may have been short (exs.) proximally, but extended beneath the tip, the inner margin a U-shaped curve, as in *Peltura* (Pl. 2, fig. 5). The width (tr.) of the inner and outer portion of each pleura is approximately equal in segments 3–12; in the first segment the inner portion is markedly narrower than the outer, in the second segment less so. Hence, the outline of the tips of segments 1–6 was only slightly convex outward (Text-fig. 1H; Pl. 1, fig. 4), while segments 7–12 decreased progressively backwards in width. The outline of the thorax was like that in the original of Text-figure 1H, not more strongly bowed outward as in the flattened original of Text-figure 1E.

The axis of the pygidium is clearly defined in the English specimens, less so in those from Newfoundland. The fulcrum lies in more than half the width of the anterior margin of the pleural region, and a facet (Text-fig. 1G) truncates the anterolateral corner of the region, the external surface being concave. The edge of the pleural region, laterally and posteriorly, appears to curve down and become vertical distally, the margin continuing the line of the pleural tips. The doublure of the pygidium is not known; possibly it was narrow, curled beneath the margin. The external surface (Pl. 1, fig. 3; Text-fig. 1G) bears fine, anastomosing ridges, subparallel to the margin and arranged in a curve concave forward on the pleural region. Similar ridges, in a curve concave forward, are present on the axial rings of the thorax, and parallel to the margin of the pleural tips. These ridges are poorly preserved, but appear to be asymmetrical terrace ridges, the steep slope facing inwards (cf. Rushton 1982, p. 52).

Enrolment. The new reconstruction (Text-fig. 2) resembles the original of Text-figure 1H, rather than the more flattened and cracked specimens from Gloucestershire (Text-fig. 1E) and Random Island

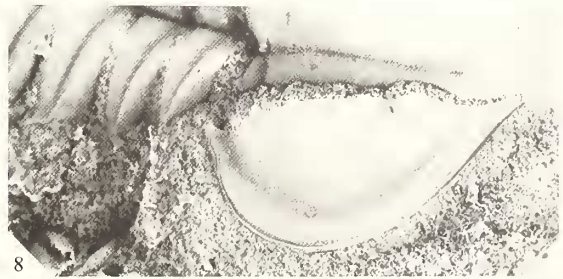
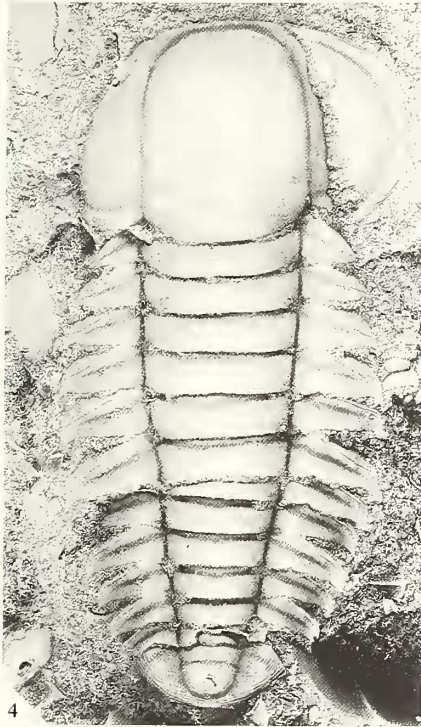
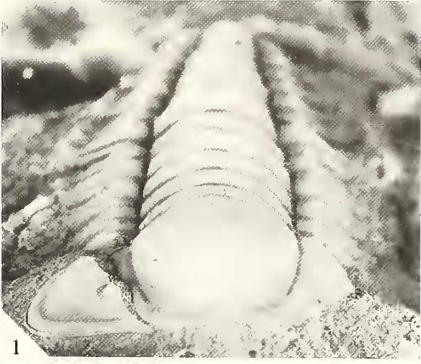
(Fortey and Owens 1991*b*, pl. 1, figs E–F), upon which Fortey and Owens' reconstruction appears to have been based. The convexity of the exoskeleton in Text-figure 2 is not unusual for some olenids, being similar to that of reconstructed olenid cephalons (Clarkson 1973), to that shown by *Peltura* (Pl. 2, figs 1–2, 4), and to that given by *Leptoplastides* by Fortey and Owens (1991*a*, fig. 9). As a consequence of such convexity, the outline of the posterior thoracic segments and pygidium is similar to that of the inner edge of the cephalic doublure (Text-fig. 2), which approximated to that of the anterior and lateral border furrows. Thus I consider that the exoskeleton was able to enroll completely, the margins of the outer edges of the thoracic pleurae and pygidium having fitted against the inner surface of the cephalic doublure, the exoskeleton forming a closed capsule. In order to achieve this closure, some 220° of flexure had to take place between cephalon and pygidium, the first 90° between the cephalon and segment 4, the flexure between segments 4 to 12 and the pygidium being less. The strong backward inclination and large size of the facets of the anterior segments, and progressive reduction in the backward inclination in successive segments is coaptative, allowing these differing amounts of flexure between sclerites. The concavity of the facets facilitated their sliding beneath the convex doublure of the posterior cephalic margin and outer portions of the pleurae, and the tips of the pleurae fitted one behind another in the fully enrolled position. The steeply down-turned edge of the pygidium came to rest against the inner edge of the cephalic doublure. If this doublure bore terrace ridges, these ridges may have interlocked with those on the pleural tips and edge of the pygidium. An analogous change of form of the size and direction of the facets is seen in *Peltura* (Pl. 2, figs 3–4), and I think it probable that this species enrolled to form a closed capsule in much the same manner. In *Triarthrus beckii* (Ross 1979, pl. 1, figs 3, 6, 9, 12) there were 14 thoracic segments, so that some 250° of flexure between cephalon and pygidium was necessary for full enrolment. In lateral view the exoskeleton had a more nearly circular outline than that suggested here for *Beltella*, and the first 90° of flexure was achieved between cephalon and third segment.

Remarks. Fortey and Owens (1991*b*, p. 74) considered that the thoracic segments of *Beltella* were like those assigned to *Acerocare tullbergi* by Henningsmoen (1957, pl. 30, fig. 9). However, the inner, horizontal portion of these latter segments constitutes most of the width (tr.), only the outermost portion is bent down, the tip bearing two short spines one on the end of each pleural band. Each band had a ridge along the crest, and the anterior band bore a narrow (exs.) articulating flange. The thorax of *A. tullbergi* is thus different from that of *B. depressa*.

Fortey and Owens (1991*b*, p. 74) gave their reasons for rejecting the subjective synonymy of *Beltella* and *Leptoplastides*, which included the 'peculiar structure' of the thorax of *Beltella*. These authors' (1991*a*, p. 449, figs 8c–j, 9) illustrations of *Leptoplastides salteri*, the type species, show that in the relative width of inner and outer portions of the pleurae, and size and shape of the pleural facets, the two type species are similar. The distinctions between them lie in the median axial spines of the occipital ring and thoracic segments, and the blunt posterolateral pleural spines of *L. salteri*.

EXPLANATION OF PLATE 2

Figs 1–8. *Peltura scarabaeoides scarabaeoides* (Wahlenberg, 1818), PMO 139.137; Upper Cambrian, zone 2d γ – δ ; Royken, Norway. 1–4, 6, 8, latex cast of external mould; 1–2, 4, anterior, right lateral, dorsal views; $\times 5$; 3, oblique, left lateral view of thorax and pygidium, showing (arrowed) sharp flexure at fulcrum of right pleurae, and left pleurae; $\times 8$; 6, oblique left posterolateral view of posterior six segments of thorax and pygidium with three spines at margin (arrowed); $\times 8$; 8, oblique anterolateral view of right free cheek and right pleurae of anterior three thoracic segments; $\times 8$. 5, incomplete, isolated left pleura of segment on same slab, excavated to reveal doublure beneath spinose pleural tip; inner margin of doublure arrowed; a = anterior articulating flange; p = posterior flange; $\times 8$. 7, isolated free cheek on same slab, oblique anterolateral view; eye lobe broken; lateral border partially removed to show flat doublure, anterior arch of border arrowed; $\times 8$.



Whether or not such distinctions are regarded as of generic significance is a matter of opinion; here I retain *Beltella*, albeit with doubt. Small pleural spines are present, for example, in the degree three meraspid stage of *Triarthrus beckii*, but are lost in later meraspid stages and the holaspid (Whittington 1992, pls 38b, 39c, 40).

Genus PELTURA Milne Edwards, 1840

Peltura scarabaeoides scarabaeoides (Wahlenberg, 1818)

Plate 2

Material. PMO 139.137, a small slab of dark grey calcareous mudstone showing the external mould of an almost complete exoskeleton, and abundant disarticulated sclerites of olenids. Most numerous are those of *P. s. scarabaeoides*, but cranidia, free cheeks and pygidia of *Sphaerophthalmus humilis*, and one thoracic segment of *Ctenopyge* type also occur. I conclude that this slab, from a loose boulder found opposite the entrance to the Slemmestad cement factory, Royken, Norway, came from rocks of the lower part of zone Vc(2d γ - δ) (Henningsmoen 1957, p. 299, pl. 5, Vc).

Description. The external mould of the complete exoskeleton closely resembles the original of Henningsmoen (1957, pl. 26, fig. 1), and is less disarticulated and more complete. In anterior view (Pl. 2, fig. 1) the steep downward curvature of the left fixed cheek is visible, the right free cheek having been displaced upwards and rotated during preservation. In its original position, the genal field of the free cheek would have sloped vertically adjacent to the lateral border, and the lateral and anterior borders would have been strongly arched in anterior view, as the detached free cheek shows (Pl. 2, fig. 7; cf. Clarkson 1973, text-fig. 4a). The doublure of the free cheek is flat peripherally, upturned at the inner margin beneath the border furrow. In his description of the eye of this species, Clarkson (1973, p. 746) noted that the external surface of the cornea was smooth, as it is in the complete specimen (Pl. 2, fig. 8) and in other, detached free cheeks.

The thorax was of 12 segments, and is disarticulated behind the sixth segment so that the seventh is partly concealed; only the left half of the twelfth segment is preserved. The inner portion of the pleura was narrow (tr.), horizontal, the outer portion sloping steeply, the anterior edge of the inner portion a flange which fitted beneath the posterior articulating flange of the segment in front. This short (exs.) posterior flange is defined by a change in slope from the inflated posterior pleural band (Pl. 2, fig. 3). A small, convex articulating process was situated at the anterior edge of the inner pleural portion, at the fulcrum, and fitted into a socket in the segment in front. The outer portion of the pleura bears a facet, the posterior edge of which, on the anterior segment, is directed strongly backward so that the pleural furrow ends against it distally. In the anterior four segments this backward inclination is progressively reduced so that the pleural furrow lies behind the facet in the fourth and succeeding segments (Pl. 2, fig. 3). Thus the facet was largest and most strongly backwardly directed on the anterior segments, proportionally smaller on more posterior segments. The tip of each segment was rounded anteriorly, drawn out into a short spine at the posterolateral angle. The doublure beneath the pleural tip has been exposed in an isolated segment (Pl. 2, fig. 5), the inner edge curved convexly outward, a narrow band extending inward beneath the facet and at the posterior edge, presumably narrowing to end before reaching the fulcrum. This specimen shows also the short (exs.) articulating flange on the anterior edge of the inner portion of the pleura, which fitted below the equally short posterior pleural flange.

The pygidium is like that of Henningsmoen's (1957, pl. 26, fig. 1) specimen, with a distinct first axial ring, the pleural region truncated anterolaterally by a facet and posterolaterally curving steeply downward. The pleural spines are partially preserved on the left side (Pl. 2, fig. 6), and were directed almost vertically downward. Anastomosing lirae run parallel to the posterolateral margin of the pygidium, and curve outward into the base of the pleural spines. Isolated pygidia in the slab also show these spines.

In the external surface of the axial exoskeleton the occipital furrow is shallow, the sigmoidal S1 faint, and S2 barely discernible. A low median tubercle is present on the occipital ring, and on each axial ring of the thorax, at the midlength in anterior segments, closer to the posterior edge in more posterior segments. The anterolateral portion of the occipital ring is gently inflated, as is the same portion of the anterior five or six thoracic axial rings. Terrace ridges, the steep slope outward-facing, are present on the outer edge and doublure of the convex cephalic border, strong and subparallel (Pl. 2, figs 7-8). A prominent terrace ridge, the steep slope backward-facing, bounds the posterior edge of the facet of each thoracic segment, with an additional one or two ridges distally curving back into the base of the spine. Lirae (symmetrical ridges) on the pleural region of the pygidium are referred to above, and are also present, curving concavely forward, on the axial ring and

terminal portion of the axis. The lirae are strongest towards the margin of the pygidium, where they appear to become terrace ridges with the steep slope forward facing.

Remarks. Although this specimen retains much original convexity, the anterior view (Pl. 2, fig. 1) shows a slight upward and outward slope of the inner portions of the thoracic pleurae, and the outer portions have a slightly concave profile distally. I attribute this, and the detachment and upward rotation of the right free cheek, to compaction. The original form would have been similar to that shown in Text-figure 2, and I consider a similar sphaeroidal enrolment to have been possible. In the closed position, the terrace ridges on the down-turned pygidial border, and on the pleural tips, would have been approximately parallel to those of the cephalic doublure. Interlocking of these ridges and grooves may thus have occurred. Bergström (1973, pl. 3, figs 1–2) figured an asymmetrically flattened specimen, and used a paper model (1973, pl. 1, fig. 7) to show sphaeroidal enrolment in this species.

Acknowledgments. I am indebted to Professor D. L. Bruton, Paleontologisk Museum, Oslo (PMO), to Dr P. R. Crowther, Bristol City Museum and Art Gallery (BRSMG), and to Dr R. A. Fortey, The Natural History Museum, London (NHM), for the loan of specimens (abbreviations used in the text for each institution are given in parentheses). Mrs Sandra J. Last prepared the text, and Miss Hilary Alberti drew Text-figure 2. I am grateful to the Department of Earth Sciences, Cambridge University, for the use of facilities, and to the Leverhulme Foundation for the support of my research. This is Cambridge Earth Sciences Publication no. 4300.

REFERENCES

- BASSETT, M. G. and COCKS, L. R. M. 1974. A review of Silurian brachiopods from Gotland. *Fossils and Strata*, **3**, 1–56, pls 1–11.
- BERGSTRÖM, J. 1973. Organisation, life and systematics of trilobites. *Fossils and Strata*, **2**, 1–69, pls 1–5.
- BURMEISTER, H. 1844. *Die organisation der Trilobiten aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Uebersicht aller zeither beschriebenen Arten*. G. Reimer, Berlin. i–xii, 147 pp, pls 1–6. [Westergaard 1947, p. 14, footnote, states that while the title page of this work is dated 1843, the back of the cover is dated 1844].
- CHATTERTON, B. D. E. and CAMPBELL, M. 1993. Enrolling in trilobites: a review and some new characters. *Memoir of the Association of Australasian Palaeontologists*, **15**, 103–123.
- CLARKSON, E. N. K. 1966. The life attitude of the Silurian trilobite *Phacops musheni* Salter, 1864. *Scottish Journal of Geology*, **2**, 76–83, pl. 1.
- 1973. Morphology and evolution of the eye in Upper Cambrian Olenidae (Trilobita). *Palaeontology*, **16**, 735–763, pls 91–95.
- and HENRY, J.-L. 1973. Structures coaptatives et enroulement chez quelques trilobites ordoviciens et siluriens. *Lethaia*, **6**, 105–132.
- ELDREDGE, N. and HENRY, J.-L. 1977. Some Phacopina (Trilobita) from the Silurian of Scotland. *Palaeontology*, **20**, 119–142, pls 18–20.
- CURTIS, M. L. K. 1968. The Tremadoc rocks of the Tortworth inlier, Gloucestershire. *Proceedings of the Geologists' Association*, **79**, 349–362, pls 8–9.
- FORTEY, R. A. 1974. The Ordovician trilobites of Spitsbergen. 1. Olenidae. *Norsk Polarinstitutt Skrifter*, **160**, 1–129, pls 1–24.
- and OWENS, R. M. 1991a. A trilobite fauna from the highest Shineton Shales in Shropshire, and the correlation of the latest Tremadoc. *Geological Magazine*, **128**, 437–464.
- — 1991b. The early Ordovician trilobite *Beltella*. *Proceedings of the Bristol Naturalists' Society* (1989), **49**, 69–79, 1 pl.
- GEYER, G. 1990. Die Marokkanischen Ellipsocephalidae (Trilobita: Redlichiiida). *Beringeria*, **3**, 1–363, pls 1–56.
- HENNINGSMOEN, G. 1957. The trilobite family Olenidae. *Skrifter utgitt av det Norske Videnskaps-Akademi i Oslo. I. Matematisk-naturvidenskapelig Klasse* **1957**, No. 1, 1–303, pls 1–31.
- HENRY, J.-L. and CLARKSON, E. N. K. 1975. Enrolment and coaptations in some species of the Ordovician trilobite *Placoparia*. *Fossils and Strata*, **4**, 87–96, pls 1–3.

- HUNT, A. S. 1967. Growth, variation and instar development of an agnostid trilobite. *Journal of Paleontology*, **41**, 203–208, pl. 22.
- JELL, P. A. 1975. Australian Middle Cambrian eodiscoids, with a review of the Superfamily. *Palaeontographica, Abteilung A*, **150**, 1–97, pls 1–29.
- LAKE, P. 1919. A monograph of the British Cambrian trilobites. Part 5. *Palaeontographical Society Monograph*, **71** (343), 89–120, pls 11–14.
- LESPÉRANCE, P. J. 1991. Vincular furrows in some early Silurian and Devonian Phacopidae (Trilobita), predominantly from North America. *Journal of Paleontology*, **65**, 276–294.
- LUDVIGSEN, R. 1982. Upper Cambrian and Lower Ordovician trilobite biostratigraphy of the Rabbitkettle Formation, western District of Mackenzie. *Life Sciences Contributions. Royal Ontario Museum*, **134**, 188 pp.
- and TUFFNELL, P. A. 1983. A revision of the Ordovician olenid trilobite *Triarthrus* Green. *Geological Magazine*, **120**, 567–577, pls 1–3.
- — 1994. The last olenacean trilobite: *Triarthrus* in the Whitby Formation (Upper Ordovician) of southern Ontario. *Bulletin of the New York State Museum*, **481**, 183–212.
- MILNE EDWARDS, H. 1840. *Histoire naturelle des crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Vol. III*. Librairie Encyclopédique de Roret, Paris, 638 pp.
- MURCHISON, R. I. 1859. *Siluria*, 3rd Edition. J. Murray, London, xix + 592 pp., 41 pls.
- NIKOLAISEN, F. 1983. The Middle Ordovician of the Oslo region, Norway, 32. Trilobites of the Family Remopleurididae. *Norsk Geologisk Tidsskrift*, **62**, 231–328, pls 1–15.
- PALMER, A. R. 1958. Morphology and ontogeny of a Lower Cambrian ptychoparioid trilobite from Nevada. *Journal of Paleontology*, **32**, 154–170, pls 25–26.
- ROBISON, R. A. 1964. Late Middle Cambrian faunas from western Utah. *Journal of Paleontology*, **38**, 510–566, pls 79–92.
- ROSS, R. J. 1979. Additional trilobites from the Ordovician of Kentucky. *US Geological Survey Professional Paper*, **1066D**, 1–13, pls 1–6.
- RUSHTON, A. W. A. 1966. The Cambrian trilobites from the Purley Shales of Warwickshire. *Palaeontographical Society Monograph*, **120** (511), 1–55, pls 1–6.
- 1982. The biostratigraphy and correlation of the Merioneth-Tremadoc Series boundary in North Wales, 41–59. In BASSETT, M. G. and DEAN, W. T. (eds). *The Cambrian-Ordovician boundary: sections, fossil distributions and correlations*. National Museum of Wales, Geological Series 2, Cardiff, 227 pp.
- SMITH, S. 1933. On the occurrence of Tremadoc shales in the Tortworth Inlier (Gloucestershire). *Quarterly Journal of the Geological Society, London*, **89**, 357–378, pl. 34.
- STITT, J. H. 1983. Enrolled late Cambrian trilobites from the Davis Formation, southeast Missouri. *Journal of Paleontology*, **57**, 93–105.
- WAHLENBERG, G. 1818. Petrifacata Telluris Svecanae. *Nova Acta Societas Regiae Scientiarum, Upsaliae*, **8**, 1–116, pls 1–4. [Bassett and Cocks 1974, p. 40, give evidence for the date of this publication].
- WESTERGAARD, A. H. 1936. *Paradoxides oelandicus* beds of Öland. *Sveriges Geologiska Undersökning, Series C*, No. **394**, 1–66, pls 1–12.
- 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. *Sveriges Geologiska Undersökning*, **C489**, 1–34, pls 1–3.
- WHITTINGTON, H. B. 1992. *Trilobites. Fossils illustrated, vol. 2*. The Boydell Press, Woodbridge, xi + 145 pp, 120 pls.

H. B. WHITTINGTON
Sedgwick Museum
Department of Earth Sciences
University of Cambridge
Cambridge CB2 3EQ, UK

Typescript received 20 February 1995
Revised typescript received 30 June 1995